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Sexual selection and the fitness consequences of male body size in the seed beetle *Stator limbatus*

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Abstract. We examined sexual selection on male body size in a laboratory population of the seed beetle, *Stator limbatus*, and the fitness consequences to females of mating with larger males. Large males produced larger ejaculates than small males. Both males and females lost body weight as a consequence of breeding, and large males lost more weight than small males. The amount of weight lost by males correlated as highly with female fecundity as did the amount of weight lost by females. Similarly, male and female body weight correlated equally highly with female fecundity. These results indicate that males make substantial contributions to female fecundity, probably through nutrients transferred in their ejaculate. As a consequence, fecundity selection should favour large body size in both males and females. We found no preference for large males when virgin females were presented with only one male, but when presented with two males simultaneously, females were more likely to mate with the larger male. This result is consistent with relative female choice or male–male competition, although no indications of male–male competition were observed. Females that mated with small males re-mated sooner than females that first mated with large males. Females that first mated with a non-virgin male were also more likely to re-mate than females that first mated with a virgin male, suggesting that females re-mate to obtain additional sperm or nutrients and not just as a form of mate choice. In addition to the possible benefits from mate choice and male–male competition, large males gain a mating advantage through reduced sperm competition. This large male advantage, combined with fecundity selection on males as well as females, may account for males being larger than females in this species.

Sexual size dimorphism is common and widespread among animals, but there is considerable variation in the nature and degree of dimorphism (Andersson 1994). In birds and mammals, males are generally larger than females (Verner & Willson 1969; Ralls 1977; Payne 1984), but in the majority of insects and other invertebrates, as well as many fish and amphibians, the reverse is true (Ghiselin 1974; Shine 1979). There have been few attempts to quantify the relative importance of different selection pressures and other factors to account for these patterns (Andersson 1994).

The common trend among insects for females to be larger than males is most frequently attributed to fecundity selection favouring large females that can lay larger or more eggs than small females (Darwin 1871; Williams 1966; Ghiselin 1974; Honěk 1993). In a number of species, female fecundity advantages may be sufficiently strong to lead to larger females even when there is sexual selection favouring large males (e.g. Vollrath 1980; Partridge & Farquhar 1983; Fairbairn & Preziosi 1996). Occasionally, sexual selection may even favour small males either through greater agility during aerial or aquatic courtship displays (Andersson & Norberg 1981; McLachlan 1987), more rapid development (e.g. selection for protandry; Singer 1982; Bulmer 1983), efficient searching for females (Fagerström & Wiklund 1982) or even through female preferences for small males (Petrie 1983; Steele & Partridge 1988).

Large male size is most commonly attributed to sexual selection in the form of male–male contest competition for access to females or to resources

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that attract females (Darwin 1871; Andersson 1994 and references therein), and possibly also endurance rivalry, whereby large males can continue courtship displays or maintain a display site for longer periods than small males (Bartholomew 1970). For example, in insects in which males have prominent weapons, such as large mandibles or horns, males are also larger than females, suggesting that male–male competition is responsible for the large size of males (Otte & Stayman 1979). Direct female preference for large males is less frequently considered as an explanation for sexual size dimorphism (but see Andersson 1994).

In many insects, males provide large ejaculates or spermatophores that, in addition to sperm, contain a substantial amount of nutrients (Thornhill 1976; Thornhill & Alcock 1983) that can be used by females for somatic maintenance and egg production. Because larger ejaculates may result in females being able to lay larger or more eggs (e.g. Ridley 1988; Fox et al. 1995b), fecundity selection may also favour males that can produce large ejaculates. Furthermore, if females mate multiply, sperm competition among males may also favour large ejaculates if ejaculate size influences fertilization success, such as through dilution of another male's sperm or by reducing the likelihood that a female will re-mate (Thornhill & Alcock 1983). If females gain a fecundity advantage from obtaining larger ejaculates, or can use the nutrients to increase longevity, then it would benefit them to select males that can provide large ejaculates. In a number of insects, more or larger spermatophores result in more or larger eggs being laid (Thornhill 1976; Thornhill & Alcock 1983; Ridley 1988; Andersson 1994). In all cases, mating with large males would be favoured if larger males are capable of producing larger ejaculates or spermatophores. Despite this prediction, few studies have demonstrated a direct advantage to mating with large males (but see Fox et al. 1995b).

We investigated modes of sexual selection for large male body size in the seed beetle *Stator limbatus* (Coleoptera: Bruchidae) in which, unlike most insects, males are larger than females, although they lack weapons. *Stator limbatus* is a generalist seed parasite widely distributed from northern South America to the southwestern United States (Johnson & Kingsolver 1976; Johnson et al. 1989; Nilsson & Johnson 1993). It is sexually monomorphic except for differences in the shape of the posterior portion of the abdomen (due to genitalia) and in body size (males are larger). Fox et al. (1995b) demonstrated that larger males produce larger ejaculates than smaller males, and that mating with large males increased a female's lifetime reproductive success. Body size is heritable in *S. limbatus* (h^2 ranges from 0.2 to 0.7; C. W. Fox, unpublished data) and other seed beetles (e.g. Messina 1993; Fox 1994), so selection on body size can result in an evolutionary response of this trait.

Sexual selection favouring larger males could take multiple forms in *S. limbatus*. If females have higher reproductive success when mating with large males, selection should favour females that preferentially mate with large males (to get large ejaculates) or mate multiply (to get multiple ejaculates). Alternatively, females could obtain the same benefits of choosing large males by taking advantage of male–male competition (such as contest competition or sperm competition) that favours large males. Large male size could also be favoured by fecundity selection through a male's contribution to female fecundity, since large males tend to contribute more biomass to egg production than small males. In *S. limbatus*, male and female body size contribute similarly to lifetime fecundity (Fox et al. 1995b), which by itself could favour sexual monomorphism.

The goals of this study were: (1) to confirm the results of Fox et al. (1995b) that females obtain a fitness benefit from mating with large males because (a) large males produce larger spermatophores, and (b) females mating with large males lay more and larger eggs than females mating with small males; (2) to determine whether there is sexual selection on male body size in *S. limbatus* favouring large males; (3) to determine what mechanisms, female choice, male–male competition, or sperm competition, are driving the evolution of large male body size in *S. limbatus*.

POPULATION ORIGIN, MAINTENANCE AND GENERAL METHODS

We collected beetles in July and August 1994 (for ejaculate size and lifetime fecundity experiments) or 1995 (behavioural experiments) from multiple localities in central Arizona. Beetles were collected by picking mature seed pods from over 50 *Cercidium floridum*, *C. microphyllum*, or *Acacia greggii* plants. We transferred mature pods to the laboratory, and seeds containing beetles were separated from uninfested seeds. The laboratory populations were initiated with over 300 field-collected individuals and reared on *A. greggii* for 2–8 generations (varied among experiments), at 29–30°C on a 16:8 h light:dark cycle prior to this study.

We initiated all experiments with virgin males and females collected from isolated seeds of *A. greggii* within 12 h of their adult emergence. Because female *S. limbatus* emerge from their host seed approximately 12–24 h prior to the initiation of egg laying and mating, and males emerge with only partially filled seminal vesicles, all virgin beetles were isolated from each other in individual 30-mm petri dishes without seeds and allowed to mature for 24–36 h before use in experiments. Thus, for all experiments, we used virgin beetles that were 24–48 h old. Each beetle was used only once. To obtain sufficient sample sizes, we needed to repeat all experiments over several days. Immediately prior to each experiment, we weighed all beetles on an electronic balance to 0.1 mg precision (behaviour experiments) or 0.01 mg precision (ejaculate size experiments).

Statistical Analyses

Because the latency to mate was highly skewed in all experiments, all analyses of this character are based on ranked data, using a non-parametric analog of an analysis of variance (Zar 1984). This technique involved rank-transforming the data and then calculating the test statistic, H=effect SS/total MS, which was compared to a chi-squared distribution. All other variables met the assumptions of the statistical tests used. Because beetle size varies with emergence time, and beetle behaviour varied among days (possibly in response to temperature and humidity variation within the laboratory), we included a date block in all ANOVAs. This date factor was frequently significant, but was statistically used only to control for variation in laboratory conditions and thus is not discussed further.

EFFECT OF MALE BODY AND EJACULATE SIZE ON FEMALE FITNESS

Experiment 1: Relationship between Male Body Size and Ejaculate Size

Methods

In seed beetles, radio-labelled nutrients in male ejaculates are incorporated into both somatic and reproductive tissues of females (Huignard 1983; Boucher & Huignard 1987), and these nutrients are used by females during egg production. Females that receive multiple ejaculates live longer, lay more eggs and lay larger eggs than once-mated females (Fox 1993a, b; Fox et al. 1995a, b). Experiment 1 was designed to estimate the relationship between a male's body size and his potential contribution to female egg production. We estimated ejaculate size by weighing females before and after mating. Before pairing, females were weighed twice to 0.01 mg precision on an electronic balance. If the two values differed by over 0.03 mg, we weighed them again. Female weight was estimated as the average of these two or three values. We checked paired beetles every 5 min until they mated, after which we re-weighed them as above. Male ejaculate size was estimated as the weight gained by the female during mating (weight of female after mating − weight of female before mating).

We examined whether larger males on average contribute larger ejaculates, and thus more nutrients, to females during mating. We also examined the relationship between male body size and total ejaculate contribution to females by males allowed to mate repeatedly with a single female. Half of the beetles (mated treatment) were paired and confined in 60-mm petri dishes with 12 *A. greggii* seeds for 5 days. At 12-h intervals we checked all dishes for eggs: beetles were briefly removed from each dish, and each seed was examined for eggs. Females oviposit directly on to seeds, so seeds bearing eggs were removed and replaced with clean seeds. We confined the remaining beetles (virgins) solitarily (as virgins) in 60-mm petri dishes with 12 *A. greggii* seeds to control for weight loss associated with dessication in the presence of dried seeds.

After 5 days (120 ± 1 h) we again re-weighed all beetles and calculated weight loss for each beetle. Females stop laying eggs after approximately

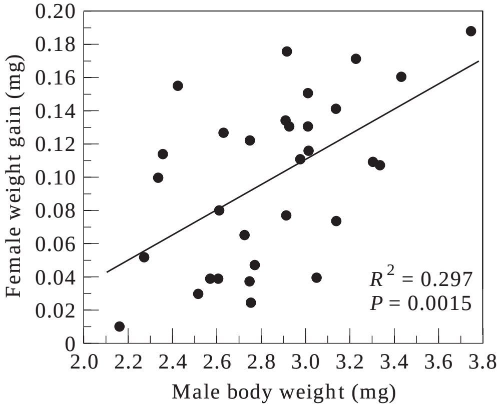

Figure 1. The relationship between male ejaculate size, measured as female weight gain during mating, and male size in the seed beetle *Stator limbatus*.

5 days, so the experiment covered nearly the entire reproductive life span of the beetles. The amount of weight lost by virgin beetles during this experiment was linearly correlated with their body size. Thus, using a linear regression analysis, we estimated the expected weight loss of a beetle as a function of body size. An individual's estimated contribution to reproduction was estimated by the difference between the expected weight loss of a virgin individual of equivalent size and the actual weight loss of a mated beetle. We then examined whether an individual's estimated contribution to reproduction was related to male body size and female lifetime fecundity.

Results

Females that mated with larger males gained significantly more weight during mating than females that mated with smaller males, suggesting that larger males are transferring larger ejaculates during mating ($R^2=0.30$, $P=0.002$; Fig. 1). The amount of weight a female gained during mating was not correlated with her own body size ($R^2=0.05$, $P=0.25$).

The amount of weight that beetles lost over 5 days (both males and females) was positively correlated with their body size (Table I). Also as expected, mated males lost more weight ($\bar{X} \pm \text{SE}=0.87 \pm 0.02$ mg) than did virgin males (0.71 ± 0.03 mg), and mated females lost substantially more weight (1.02 ± 0.02 mg) than did virgin females (0.54 ± 0.02 mg).

Table I. Analysis of covariance for the effects of body size, sex and mated status (mated or virgin) on weight loss over 5 days by the seed beetle, *Stator limbatus*

Variable	$F_{1,109}$	P
Sex	5.20	0.025
Body weight	118.8	<0.001
Mated status	201.9	<0.001

An examination of female weight loss over 5 days indicates that, after correcting for weight loss due to somatic maintenance and dessication, large females contributed more biomass to reproduction than small females ($R^2=0.306$, $P<0.001$). Large females also laid more eggs than small females ($R^2=0.246$, $P=0.001$), and fecundity was positively correlated with the weight a female lost as a result of reproduction ($R^2=0.322$, $P<0.001$; Fig. 2). The amount of weight lost by males as a result of reproduction (after correcting for weight loss due to somatic maintenance and dessication) was positively correlated with their body size ($R^2=0.559$, $P<0.001$) and positively correlated with the number of eggs their mates laid ($R^2=0.276$, $P<0.001$; Fig. 2). In fact, the R^2_{partial} between male weight loss due to reproduction and his mate's fecundity, and the R^2_{partial} between female weight loss due to reproduction and her fecundity, were similar (Table II). Using virgin males as a baseline for metabolic weight loss probably leads to an underestimation of the contribution to reproduction by mated males. Virgin males lost more weight than did virgin females ($F_{1,33}=33.6$; $P<0.001$; Fig. 3), probably because unmated males were more actively searching for females. Following mating, males tend to become inactive and stop searching for females (personal observations), probably resulting in a lower metabolic rate for mated males. Although our method probably underestimates male contribution to reproduction, it demonstrates that the relationship between male size and contribution to reproduction is highly positive.

These results imply that: (1) large males expend more biomass on reproduction than do small males; (2) this increased biomass expenditure affects female lifetime fecundity; and (3) male *S. limbatus* contribute as much biomass to egg production as do females.

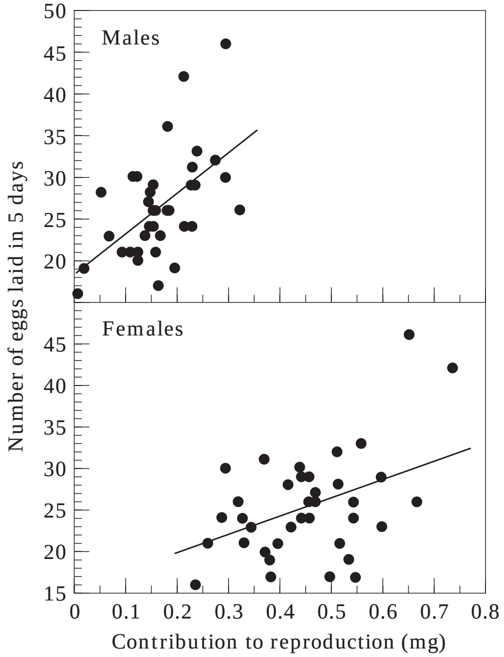

Figure 2. The relationship between a female's fecundity and her (female) and her mate's (male) contributions to reproduction (weight loss after correcting for natural weight loss due to metabolism and desiccation) over 5 days (see Table II).

Table II. The simultaneous effects of male and female contributions to reproduction (weight loss after correcting for natural weight loss due to metabolism and desiccation) on female fecundity over 5 days

Variable	Squared partial correlation	*P*
Male weight loss	0.315	<0.001
Female weight loss	0.358	<0.001
		$r^2=0.522$

Experiment 2: Male Body Size Effects on Female Fecundity

Methods

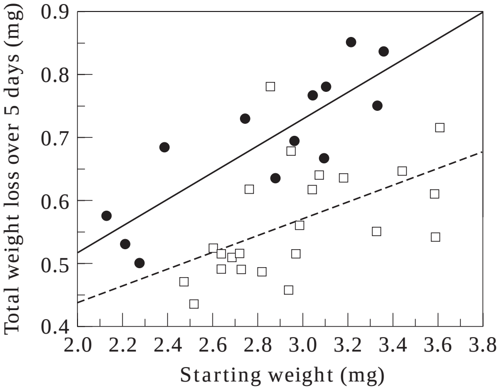

Figure 3. The relationship between body size and total weight loss (due to metabolism and desiccation) over 5 days for virgin male (—●—) and female (– –□– –) *Stator limbatus*.

Fox et al. (1995b) demonstrated that female *S. limbatus* mated with large males laid more and larger eggs than females mated with smaller males, demonstrating an advantage to preferentially mating with large males. Here we attempted to confirm these results. To quantify the effects of male body size on female fecundity and egg size, we randomly paired a single virgin male with a single virgin female and confined them in a 60-mm petri dish containing 12 *A. greggii* seeds ($N=55$ and 76 pairs in each of two replicates). At 12-h intervals until all females died, all dishes were checked for eggs, and seeds bearing eggs were removed and replaced with clean seeds. We measured the length and width of eggs laid in the two replicates using an ocular micrometer on a stereomicroscope (two randomly chosen eggs laid during the first 12 h after the initiation of egg laying were measured for each female).

Results

In both replicates, *S. limbatus* females mated with larger males laid significantly more eggs over their lifetime than did females mated with smaller males (Fig. 4). In a multiple regression analysis, the partial effects of both male and female body sizes on lifetime fecundity were both large and of the same magnitude for both sexes (Table III), suggesting that males contribute as much to female egg production as do females. This result is in agreement with those of experiment 1, which indicated that larger males lost more weight due to reproduction than smaller males, and that the amount of weight they lost due to reproduction was correlated with the number of eggs their mate laid.

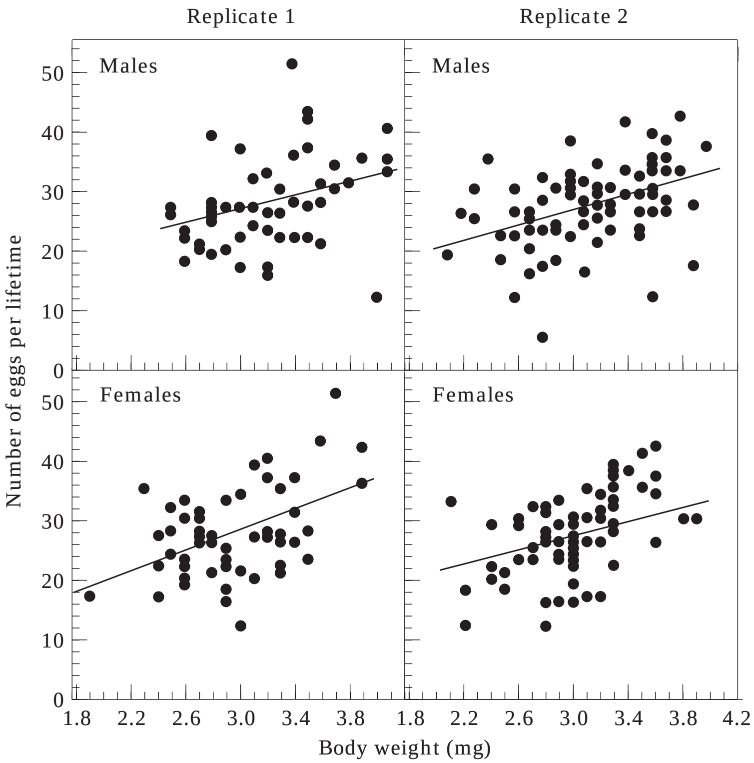

Figure 4. The relationship between a female's lifetime fecundity and her (female) and her mate's (male) body size for two replicates (see Table III).

Table III. The relationship between paternal and maternal body size (weight) and female lifetime fecundity and egg size (length and width) for two replicates

Variable	Lifetime fecundity: Squared partial correlation	Lifetime fecundity: P	Egg length: Squared partial correlation	Egg length: P	Egg width: Squared partial correlation	Egg width: P
Replicate 1 ($N=55$)						
Paternal weight	0.209	<0.001	0.016	0.35	0.003	0.68
Maternal weight	0.287	<0.001	0.005	0.59	0.002	0.77
		$r^2=0.36$		$r^2=0.02$		$r^2=0.00$
Replicate 2 ($N=76$)						
Paternal weight	0.135	0.001	0.019	0.24	0.004	0.57
Maternal weight	0.101	0.005	0.031	0.13	0.016	0.27
		$r^2=0.23$		$r^2=0.03$		$r^2=0.02$

Although male body size had a large effect on female fecundity, we could detect no effect of male body size on the size of a female's eggs (Table III). This finding is contrary to the results of Fox et al. (1995b) which suggested that egg size was affected by male body size, although that effect was small and only weakly significant.

SEXUAL SELECTION ON MALE BODY SIZE

Experiment 3: Effect of Male Size on the Latency to Mate

Methods

To determine whether females mated with large males were more likely to mate, or mated more quickly, than females paired with small males, that is, whether females showed an absolute mate preference for large males in the absence of male–male competition, we confined virgin females with a single virgin male and examined the latency to mating. We transferred randomly selected males into a 30-mm petri dish containing a virgin female (without seeds) and placed them in a 29–30°C incubator. We checked dishes every 3 min until the pair mated. Because matings last about 5 min, this schedule ensured that we observed all matings. Pairs that failed to mate within 4 h were classified as 'unmated'. The females of these pairs were confined on *A. greggii* seeds for at least 2 days to verify that they were still virgin (unmated females rarely lay eggs) to confirm that no matings had been missed during the experiment.

Results

We tested 38 females, of which 29 (76%) mated during the first 4 h after being paired with a single male. None of the 'unmated' females subsequently laid any eggs, indicating that we did not miss any matings. There was no significant difference between pairs that mated within 4 h and those that did not in either male body size ($\bar{X}_{\text{mated}}=$ 3.4 mg; $\bar{X}_{\text{unmated}}=3.2$; two-way ANOVA: $F_{1,35}=0.42$, $P=0.52$) or female size ($\bar{X}_{\text{mated}}=3.2$; $\bar{X}_{\text{unmated}}=3.2$; $F_{1,35}=0.069$, $P=0.79$). Among pairs that mated, there was no relationship between the latency to mate and male body size (non-parametric ANOVA: $H=1.91$, $P=0.18$).

We also compared the size of males that mated quickly (i.e. within the first 15 min of pairing) with those that mated more slowly or not at all. To obtain a larger sample size, we pooled the results from this experiment with the results of the first (virgin) mating from experiment 5 (below). Again, there was no evidence that male size affected whether a pair mated (male size: $F_{1,163}=2.26$, $P=0.13$; female size: $F_{1,163}=0.24$, $P=0.63$).

Experiment 4: Female Choice of Two Males

Methods

To examine the potential role of relative female choice or male–male competition in obtaining matings, we paired virgin females with two virgin males. All males used in this experiment were ranked according to their size and divided into two groups, representing the largest half and smallest half of the size distribution. To ensure a reasonable size difference between paired males, the largest of the large males and the largest of the small males were confined simultaneously with a randomly selected female. Next, the second largest of the large males and the second largest of the small males were confined with a second randomly selected female, and so on until all males were confined with another male and a female. This approach enhanced our ability to detect statistically any effect of body size and enabled us to determine easily which male successfully mated without marking the males.

We continuously observed the trios (two males + one female) for the first 20 min and then placed them in a growth chamber at 29–30°C and checked them every 3 min until they mated (up to 4 h). When a male successfully mated, the time of mating was recorded, and the unmated male was removed and re-weighed to determine his identity. We then determined whether the small or large males were relatively more successful in obtaining matings.

Results

Females mated in 41 of 51 mating trials in which they were presented simultaneously with two males (80%). The large male mated in 27 trials, but the small male mated in only 14 (one-tailed sign test, $P=0.03$). Neither the winner's weight, the loser's weight, nor the difference between them was correlated with the latency to mating ($P>0.6$ for all). This result is consistent with relative female choice (females comparing among males), but it could also be due to male–male competition. Scramble competition that favours large males seems unlikely, since we would expect smaller latencies for large males in the one-male experiment as well. We observed no overt competitive behaviour among males, such as fighting or courtship interference.

Experiment 5: Effect of Male Size on Female Re-mating

Methods

Although experiments 3 and 4 provide information about sexual selection on male body size in *S. limbatus*, they do not allow us to distinguish the roles of female mate choice for large males from effects of male body size on male mating behaviour and male–male competition. This experiment was designed to examine selection on male body size mediated through female re-mating behaviour by quantifying the effect of a male's body size on the tendency of a female to re-mate when she encountered a new male. We randomly paired females with a single male, as in experiment 3, and checked them every 3 min until they mated. Because of constraints of time and the availability of sufficient males, we monitored these first pairs for only 1.5–2 h. Immediately following mating, the male was removed and a second randomly assigned male was placed with the female. This pair was returned to the incubator and checked every 3 min, up to 4 h or until they mated. We recorded whether a female re-mated and the time at which the female re-mated. In subsequent statistical analyses, we tested whether females that mated first with a small male tended to re-mate more often and sooner than females that first mated with a large male.

Results

Of 60 virgin females that were presented sequentially with two males, 38 (63%) re-mated when presented with the second male. The size of the first male, but not the size of the second male, influenced how quickly a female re-mated. As expected, females first mating with smaller males re-mated sooner than females first mating to a larger male (Table IV). There was also a significant first male–second male interaction (Table IV), but we have no interpretation of this interaction. Female body size had no detectable effect on her tendency to re-mate.

Table IV. Non-parametric analysis of covariance (see text) for the effects of female weight and the weight of the first and second males on the latency to mating with the second male by female *Stator limbatus*

Variable	*H*	*df*	*P*
First male weight	9.76	1	0.002
Second male weight	2.63	1	0.11
Female weight	1.97	1	0.18
Date block	8.02	4	0.09
First male weight$*$second male weight	9.13	1	0.003

Experiment 6: Effect of Male Mating History on Female Re-mating

Methods

One likely explanation for why females mating first with small males are more likely to re-mate, and re-mate sooner, than females mating first with large males is that small males donate smaller ejaculates to females during mating. This experiment was designed to examine that hypothesis by varying male ejaculate size independent of male body size. To do this, we compared the tendency of a female to re-mate when she encountered a new male if she had first mated with a virgin male (with full seminal vesicles) or with a non-virgin male (partially depleted). To control for male body size, we used a paired design in which a single male was mated to two females. The first female in this pair thus mated with the male when he was a virgin and the second mated with him after he had previously mated. If a male did not re-mate, he was excluded from the analyses.

As in experiment 5, we randomly paired males with a single female and checked them every 3 min until they mated. Following mating, the male was confined with a second female, and again checked every 3 min until they mated. Immediately after their first mating, each of these females (mated to a virgin and non-virgin male, respectively) were confined with a new, randomly selected virgin male and checked every 3 min for mating for up to 4 h. As in previous experiments, we recorded whether a female re-mated. In subsequent statistical analyses, we tested whether females that mated first with a non-virgin male were more likely to re-mate than females that first mated with the same male when he was virgin. We compared re-mating by first and second females with a Wilcoxon signed-ranks test by assigning a value of 1 to females that re-mated and 0 to females that did not re-mate.

Results

Once mated, males did not readily re-mate (only 16 of 74 mated males re-mated within 4 h), resulting in small sample sizes for this experiment. Females mated to a virgin male re-mated in seven of 16 trials; the female mated to a non-virgin male re-mated in 13 of those trials (Wilcoxon signed-ranks test, one-tailed, $Z=1.90$, $P=0.029$). There were too few trials ($N=5$) in which both females of the pair (see Methods) re-mated to test the effect of male mated status on the latency to re-mate.

DISCUSSION

Females receiving multiple male contributions lay more (Ridley 1988) and often larger eggs (Fox 1993b) than do once-mated females, suggesting large effects of male-derived nutrients on female reproduction. What has not been demonstrated often in insects is that females gain direct fitness advantages from mating with specific (in this case, larger) males (e.g. Pitnick 1991; but see Gwynne 1988; Reid & Roitberg 1995). Our results confirmed Fox et al.'s (1995b) finding that female *S. limbatus* gain a fitness advantage from mating with large males (Fig. 3, Table III). This fitness advantage was detected as an increase in female fecundity with an increase in male size. Contrary to Fox et al. (1995b), however, we did not observe an increase in egg size with increased male size.

Several explanations could account for these results. First, females mating with large males may obtain more nutrients via the male's ejaculate, either through larger per-ejaculate contributions, as is suggested by the positive relationship between male size and ejaculate size (Fig. 1), or by increased frequency of mating, although videotaped observations of paired beetles revealed no relationships between the number of matings and either male size or female fecundity (Fox et al. 1995b). Second, the increase in fecundity could reflect cryptic female choice (Eberhard 1996), with females investing more in reproduction when mated to a preferred (larger) male. Third, larger males might transfer a non-nutritive substance such as a pheromone that enhances egg laying in females. We do not have data to test the latter two hypotheses; although these hypotheses may explain the short-term phenology of egg laying, we doubt that they are sufficient to account for variation in total lifetime fecundity, since females do not feed and thus have a fixed amount of resources available for reproduction. For this reason, and the fact that females of other seed beetles incorporate nutrients from male ejaculates into their somatic and reproductive tissues (Huignard 1983; Boucher & Huignard 1987), we believe that the increased fecundity as a consequence of mating with large males is probably mediated by large males providing more nutrients to females in their ejaculate.

Not only do large males contribute more to female fitness than do small males, but male contributions to female fecundity (weight loss corrected for metabolism and dessication) are similar in magnitude to female contributions (Table II), as are the effects of male and female body size on total fecundity (Table III). These results suggest that fecundity selection on body size should be very similar for both males and females, and hence cannot account for sexual size dimorphism.

Although females benefit from mating with large males, we detected no female preference for large males, measured as the latency of virgin females to mate when presented with a single male. Females none the less may tend to mate with larger males if presented with a choice of males or as a result of male–male competition. When two males were placed together with the female and competition was allowed, females were more likely to mate with the larger male. These results are consistent with male–male competition but are also consistent with female choice in which there is a relative mating preference. If females compare among males simultaneously or compare a male with the average of previously encountered males, then a preference could be detected when presented with two (or more) males but not when presented with only one male.

The large male advantage in the two-male experiment could also be due to some form of male–male competition, such as direct contests among males, courtship interference or scramble competition. The data do not appear to support scramble competition, since there was no evidence that big males are better at seeking or pursuing females (one-male experiment). We observed no overt male–male aggression or courtship interference, but we cannot exclude more subtle forms of male–male competition such as pheromonal signalling (e.g. Boppré 1984; Moore & Breed 1986). Additional observation and experimentation of courtship interactions are necessary to clarify the importance and form of male–male competition.

In addition to being more successful at obtaining matings, large males gain an additional advantage in that females are less likely to re-mate if they first mated with a large male. If this species has last-male sperm precedence, as is the case in other seed beetles (Eady 1994), then this benefit may be considerable (unless large males have a lower rate of fertilization immediately following mating, which seems unlikely). Females may be less likely to re-mate after mating with a large male due to mate choice, with females attempting to ensure that their offspring obtain the high-quality genes of the first male; alternatively, they may be less likely to re-mate because they have little additional storage space or need for more ejaculate. In *C. maculatus*, virgin males produce larger ejaculates than do non-virgins (Fox et al. 1995a) and, given the reluctance of males to re-mate, this seems likely for *S. limbatus* as well. Females mated to non-virgin males were more likely to re-mate than females mated to virgins, suggesting that female re-mating is determined by how much ejaculate they obtained in their first mating rather than some other aspect of male quality.

Based on our findings, the larger-male sexual dimorphism of *S. limbatus* can be accounted for by a combination of either direct male–male competition or female choice favouring large males plus the decreased risk of sperm competition for large males due to reduced female re-mating. This conclusion is consistent with that of many other studies that have attributed large male size to male–male competition or to female choice (reviewed in Andersson 1994; Fairbairn & Preziosi 1996). In insects, however, most males are smaller than females. This size disparity is most commonly attributed to fecundity selection favouring larger females (Darwin 1871; Williams 1966; Ghiselin 1974; Honěk 1993). *Stator limbatus* is unusual in that males are larger than females. We suggest that the large male size of this species is due in part to the large male contribution to female fecundity, with fecundity selection acting equally on both males and females resulting in size monomorphism, and sexual selection favouring large males, which provides the additional advantage that results in male-biased size dimorphism.

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